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Natural reward drives the advancement of life

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Abstract

Throughout the history of life on earth, rare and complex innovations have periodically increased the efficiency with which abiotic free energy and biotic resources are converted to biomass and organismal diversity. Such macroevolutionary expansions have increased the total amount of abiotic free energy utilized by life and shaped the earth's ecosystems. Meanwhile, Darwin's theory of natural selection assumes a historical, worldwide state of effective resource limitation, which could not possibly be true if life evolved from one or a few original ancestors. In this paper, I analyze the self-contradiction in Darwin's theory that comes from viewing the world and universe as effectively resource limited. I then extend evolutionary theory to include a second deterministic evolutionary force, **natural reward**. Natural reward operates on complex inventions produced by natural selection and is analogous to the reward for innovation in human economic systems. I hypothesize that natural reward, when combined with climate change and extinction, leads to the increased innovativeness, or what I call the **advancement**, of life with time. I then discuss applications of the theory of natural reward to the evolution of evolvability, the apparent sudden appearance of new forms in the fossil record, and human economic evolution. I conclude that the theory of natural reward holds promise as an explanation for the historical advancement of life on earth.

Keywords

invention, entrepreneurship, innovation, success, progress, advancement

Introduction

Charles Darwin, in "The Origin of Species", derived a radical new theory using an analogy between artificial selection and a hypothetical force of nature that he called **natural selection** (Darwin 1859). Darwin's analogy has proven so powerful in under-

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standing evolutionary change that scientists now speak of natural selection as if it is a true force of nature, rather than a concept that Darwin created. Yet, Darwin uniquely developed the metaphor of natural selection, departed from the normal scientific methods by devising a rash new framework, and revolutionized the way that facts were taken to support a theory.

After over 150 years of development, Darwin's theory has now fulfilled the destiny that Huxley (1880), p. 549 anticipated. Starting as heresy, it has now become a doctrine that is accepted with as little reflection as Darwin's contemporaries once rejected it. The main doctrine that is uncritically accepted is that natural selection is the only non-random, lawlike (deterministic) force of evolution, and is complemented only by random forces-like mutation, recombination, and genetic drift (Simpson 1944, 1949, 1953; Dobzhansky 1951; Stebbins 1959).

In our modern world of rapid human technological evolution, we are now positioned to ask whether Darwin's theory might be extended fruitfully to cover deep evolutionary time. Recently, human technological evolution has revealed themes that occur millions of times faster in human culture compared to organic evolution. There is a parallel, for example, between the large-scale expansion of human economies and terrestrial ecological diversity (Fig. 1). The rate at which whole new technologies originate, spread, and go obsolete is known to anyone who owns a computer or smartphone.

In this paper, I outline a theory of evolution based on a metaphorical link between the reward for innovation in human societies and a force of nature that I call **natural reward**. I adopt Darwin's approach of inventing a new theory, and then asking how it illuminates various classes of phenomena. I will begin by explaining how a self-contradiction in Darwin's theory created a schizophrenic state of modern evolutionary theory. I will then show how a proper understanding of Darwin's theory allows us to

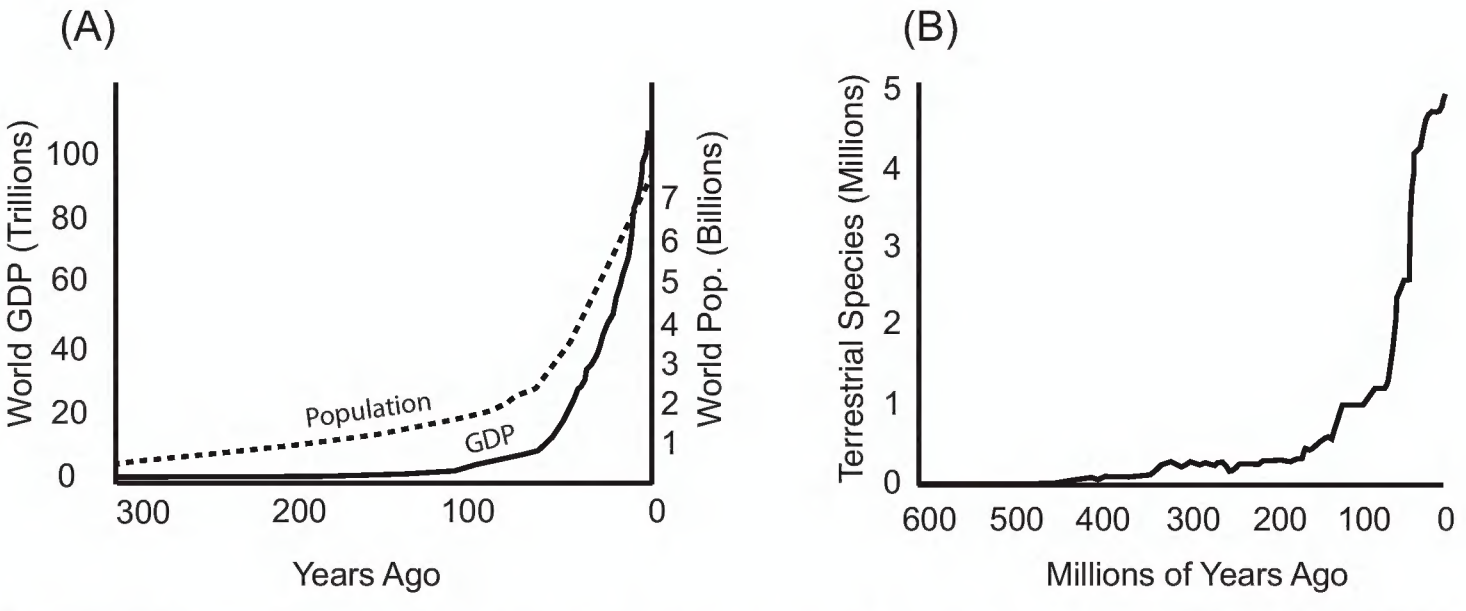

Figure 1. Expansion in **A** human economies, as represented by world gross domestic product (GDP), measured as the total monetary or market value of all the finished goods and services produced, and population **B** nature, as measured by the number of terrestrial animal species **A** redrawn from ourworldindata.org **B** redrawn from Benton (2016).

break free of the delusions and abnormal interpretations of reality that come from the uncritical acceptance of both of Darwin's conflicting messages. I finally outline a new theory, based on an alternative deterministic force of evolution, **natural reward**, which I propose acts synergistically with natural selection.

The Darwinian double bind

A **double bind** is a dilemma in communication in which an individual or group receives two or more conflicting messages from an authority, which the receiver cannot resolve or opt out of (Bateson et al. 1956). Bateson et al. (1956) argued that double binds imposed on children can lead to the development of schizophrenia, a mental disorder characterized by abnormal interpretations of reality, disorganized thinking, and delusions. I argue that Darwin, by giving conflicting messages, created a double bind for modern evolutionists.

Darwin's double bind manifests as the conflicting messages that: (i) natural selection yields comparative progress only, and (ii) natural selection also yields absolute progress (Box 1). The authors of the modern synthesis could not comment on the contradiction without revealing a weak point of evolutionary theory to political and religion-based ideological opponents, who promoted the teaching of pseudoscience in high school classrooms (Tax and Callender 1960b; p. 42). Therefore, the authors of the modern synthesis accepted both messages as correct, and thus in fighting pseudoscience, advocated a theory that contradicted itself (e.g., Simpson 1949, p. 269; Dobzhansky 1951, p. 17; Stebbins 1959, pp. 305–306). Evolutionists since that time have accepted both contradictory messages in various ways (Ruse 1993, 1996), in some cases apparently unaware of the contradiction. This led to a schizophrenic state of modern evolutionary theory.

This schizophrenia is characterized by the metaphysical delusion of teleology. **Teleology** is the doctrine that **final causes exist, and that the study of apparent design in nature provides evidence for final causes**. Today in evolutionary theory, teleological research programs explain the existence or ubiquity of complex traits by appeal to final causes. They do so by a sequence of habits. The first habit is to take the apparent design function of a trait as the cause for its existence. I call this invoking a **design-function** final cause. The second habit is to causally link the design function to the cause for existence by a general principle, like "fitness maximization" (Ayala 1970; Grafen 2014). I refer to this habit as invoking a **unifying** final cause. The third habit is to take apparent design in nature as evidence of a unifying final cause, and by implication, a design-function final cause. I call this habit **teleological empiricism.**

An example of these habits culminating in teleological empiricism comes from the study of kin recognition. Here, the first habit is to assume that kin recognition evolves for the apparent design function of directing help to kin (Grafen 1990). The second habit is to link the design function to the cause for existence by the unifying final cause of inclusive fitness maximization (West and Gardner 2013; Grafen 2014).

The third habit is to take apparent design of kin recognition in nature as evidence for the unifying final cause (Fletcher and Michener 1987, p. 419), and by implication, the design-function final cause.

The result of the persistence of teleological thinking in prominent fields of evolutionary biology is that the current climate is much like it was immediately after the publication of "The Origin of Species". In that era, researchers disagreed about whether Darwin had supported or replaced teleology (Huxley 1870, p. 330). Likewise, evolutionists today still debate how Darwin's theory relates to teleology (Ayala 1970; Ghiselin 1994; Huneman 2019). I therefore will close the door to teleological interpretations of natural selection by first explaining the importance of the struggle-for-existence metaphor for Darwin's theory.

Box 1. The Darwinian Self-Contradiction.

Ruse (1993), p. 58 pointed out that Darwin tried to get *absolute* progress from *comparative* progress, where *comparative* progress involves the adaptive advance of one line of organisms over others, and *absolute* progress involves improvement on a scale of fixed value. In our modern understanding of evolution, *comparative* progress refers to the adaptive replacement of one allele by another. For example, an allele for non-cooperation might replace an allele for cooperation in an environment characterized by frequent associations with non-relatives (Gilbert et al. 2007). An allele for non-cooperation may thus be progressive with respect to the immediate social environment, but may lead to extinction (e.g., Fiegna and Velicer 2003). Whether natural selection leads to continued population survival or extinction may depend on the arbitrary state of the environment (Travisano et al. 2018; Svensson and Connallon 2019).

With respect to *comparative* progress, Darwin stressed that natural selection acts only by the accumulation of slight modifications of structure or instinct, each profitable to the individual under its conditions of life (Darwin 1859, pp. 170, 233, 235, 435), that natural selection produces only relative perfection and that true wonder is why imperfection is not more commonly observed (Darwin 1859, p. 472), and that natural selection, though sometimes leading to advancement, includes no necessary law of advancement – and could just as easily lead to retrogression (Darwin 1859, p. 133, 137). With respect to *absolute* progress, on the other hand, Darwin argued that species going extinct would tend to have an inferiority held in common (Darwin 1859, pp. 321–322, 327, 344), that those rising to dominance would have a superiority held in common (p. 128), and that natural selection causes newer forms to supplant their less-improved ancestors (pp. 5, 108, 119, 126–128, 337).

In an 1854 letter to Hooker, Darwin said, "With respect to 'highness' & 'lowness,' my ideas are only eclectic & not very clear" (Darwin-Hooker 27 Jun 1854). Nevertheless, throughout his works, Darwin never commented on the inconsistency between absolute perfection and relative perfection. Instead, in later editions of *The Origin*, Darwin argued that the "improvement" caused by natural selection, "inevitably leads to the gradual advancement of the organization of the greater number of living beings throughout the world" (Darwin 1876, p. 97).

The struggle for existence

Evolutionists since Darwin have relied on the foundations that Darwin provided with the struggle for existence metaphor, without understanding its importance. Fisher (1953), p. 5 argued that Darwin's notion of the struggle for existence was a "journalistic slogan" that Darwin used to get his doctrine across to a "thick-headed audience." Dobzhansky (1951), p. 77 asserted that Darwin's metaphors were "more picturesque than accurate," and Lewontin (1970), p. 1 that the idea of competition for resources in short supply was "not integral" to Darwin's argument. Textbooks today teach the conditions for natural selection with no mention of the struggle for existence or resource limitation (e.g., Freeman and Herron 2007, pp. 76–77; Barton et al. 2007, pp. 458, 460, 474; Bergstrom and Dugatkin 2011, p. 63–64). I therefore will first review the importance of Darwin's struggle for existence metaphor for his theory. I will then disprove Lewontin's (1970) arguments against it.

To begin with, the struggle for existence metaphor determined how Darwin applied his theory to comparative progress. In adopting Malthus's doctrine and applying it to nature, Darwin derived two arguments. First, Darwin suggested that the world was already resource limited (Fig. 2A). Darwin (1859), p. 67 captured his worldview by stating, "The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows…" Therefore, "… from the high geometrical powers of increase of all organic beings, each area is already fully stocked with inhabitants, it follows that as each selected and favoured form increases in number, so will the less favoured forms decrease and become rare" (p. 109). Thus, the world is already packed with wedges, and the placement of a new wedge (species) requires either tighter wedging, or that a wedge is thrust out by extinction (Stauffer 1975, pp. 208, 631).

In some other passages, however, Darwin reasoned that unrestricted increase would lead to the earth being covered by the progeny of a single pair of organisms, however slow breeding (Darwin 1859, p. 64). In that case, climatic variability (p. 68), climatic extremes (p. 69), microbial epidemics (p. 70), or parasitic insects (p. 72), prevent the ultimate check of limited food (p. 68; Fig. 2B). Darwin (p. 74) thus suggested that for any given species, "…many different checks, acting at different periods of life, and during different seasons or years, probably come into play…"

In either case, Darwin used his assumption of effective resource limitation to define the form of competition. Darwin argued that the struggle for existence is most severe among those competing for the same resources (Darwin 1859, pp. 68, 75, 76, 121, 320, 468), and identified the **species** as the **set of individuals closely resembling each other** (pp. 52, 481), which are **discrete compared to other sets** (p. 482). Darwin then reasoned that evolution by natural selection is a within-species process, because only types within species are near enough in their resource requirements to competitively displace each other (pp. 4, 5, 75–76, 80–130; see also Fisher 1930, p. 121).

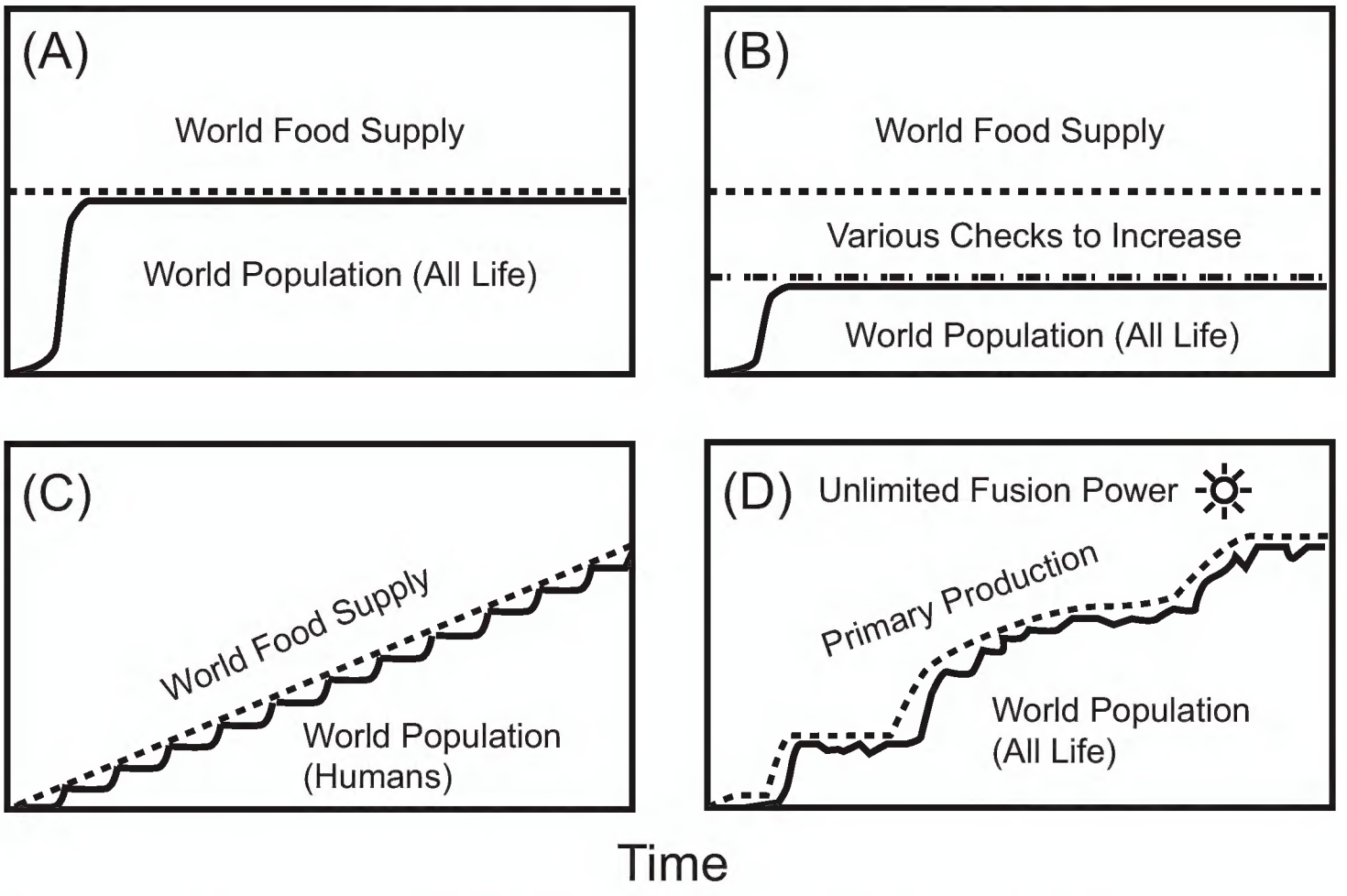

Figure 2. Different perspectives on the world resource supply. A Darwin's first argument assumes population have hit the ultimate limit of food supply. The placement of a new wedge (species) requires that another be thrust out by extinction. **B** Darwin's second argument assumes that the ultimate check of limited food is not reached because of various other checks to increase. **C** Malthus assumed that populations are continually in a state of effective resource limitation even though the food supply is increasing, because linear increases of food are quickly exhausted by the exponential population increases that they cause. **D** There is an unlimited abiotic resource supply, and the biotic "food supply" is increasing by innovations in primary production.

Darwin also reasoned that because members of the same species are similar in their resource requirements, their variations would be slight (Darwin 1859, pp. 81–86), and modifications of form and function gradual (Darwin 1859, pp. 186–190, 233–235; see also Fisher 1930, pp. 38–41).

Lewontin (1970), in contrast, proposed that the only condition for natural selection is heritable variation in **fitness**, with **fitness** defined as **net reproductive success** (*sensu* Fisher 1930, p. 34). Lewontin did not include the struggle for existence in his conditions for natural selection, and this omission meant that it was no longer clear that natural selection applies only within species. Instead, it seemed that natural selection might apply to any level with heritable variation in "fitness" (e.g., possibly species, phyla, and ecological communities; Lewontin 1970). Therefore, it is important to examine Lewontin's argument for why the struggle for existence can be ignored. Lewontin's first argument is that resource limitation is unnecessary for organisms to struggle for existence because, as Darwin argued, factors other than limited food (e.g., limited water, parasites, predators) might check populations (see above). A plant on the edge of the de-

sert may be said to struggle against the drought because in that case, moisture limitation rather than food limitation provides the main check to population increase (Lewontin 1970, p. 1; Darwin 1859, p. 62). However, Darwin (1859) assumed an "extreme limit" of a fixed food supply (p. 68), whether or not the population was actually checked by food limitation (Fig. 2A, B) or other factors (Fig. 2B). Therefore, Lewontin overlooked the importance of the extreme limit of food in Darwin's argument, which then caused Lewontin to dismiss the importance of the struggle for existence.

Lewontin's second argument examines the extreme situation in which not even food checks a population. Here, Lewontin argued that if two bacterial strains are growing exponentially in an excess of nutrients and one strain grows faster than the other, then natural selection has happened between the different strains. Lewontin took this to suggest that natural selection would happen even without checks to increase, thus apparently disproving the importance of the struggle for existence in defining the levels of selection. However, Lewontin's argument can be scrutinized by taking the thought experiment to its logical extreme. If the strains continued to grow in an abundance of nutrients indefinitely, neither strain would ever displace the other. Without any competitive displacement of types, it is unclear how evolution by natural selection could happen. If food became limited, moreover, natural selection would not necessarily act between the strains. If the strains use the same resources differently, or depend on different resources (e.g., one feeds off the metabolic byproduct of the other; Blount 2017), they may persist indefinitely as separate species. In that case, the different strains would evolve by natural selection separately, because the struggle for existence would happen only within a strain. In other words, the struggle for existence would still determine the levels at which natural selection acts, just as Darwin argued.

Thus, Darwin's reasoning from the struggle for existence justified his application of natural selection to the gradual adaptation of species to their immediate environments and thus to comparative progress (Box 1). Reasoning from the struggle for existence, there were only two ways that absolute progress could happen. Under Darwin's first perspective (Fig. 2A), evolution over many thousands of generations may yield a tighter wedging. Thus, Darwin argued that a greater amount of life could be supported with a greater diversity of species (Darwin 1859, p. 114). Under Darwin's second perspective (Fig. 2B), long-term evolution may yield an increase of population, for example if a release from alternative checks to increase allows the world population to come closer to the ultimate check of limited food. Yet, although Darwin sometimes referred to population increase (Darwin 1859, p. 102, 119, 472), he never discussed whether there was some greater untapped resource supply (Fig. 2C, D), as would be necessary for the expansion of all life on earth from one or a few original forms (Darwin 1859, p. 491).

The struggle for supremacy

In contrast to Darwin, Malthus (1826) explicitly allowed an increase in the food supply (Fig. 2C). However, Malthus considered human populations, and his assumption

of increases of food supply was warranted by innovations in agriculture. If life had expanded from a few simple ancestors, however, life's "food supply" must have increased. In this section, I will briefly review the basic ways that life's food supply has increased and how this relates to an alternative struggle of life.

To begin with, early life used geothermal sources of energy and only later gained the ability to use solar power (Judson 2017). A major increase of the resource supply came when photosynthesis first originated in anoxygenic form, about 3.7 Gy (Judson 2017). Another major step came 2.45–2.32 Gy, with the origin of modern oxygenic photosynthesis, which uses the energy from light to split water and make glucose as food (Judson 2017). During the Jurassic and early Cretaceous 200–130 My, a reduction of genome and cell size in angiosperms allowed optimization of C3 photosynthesis (Simonin and Roddy 2018; Gago et al. 2020). Even in the past 1% of life's history (40 million years), a reduction of atmospheric CO_2 combined with increased aridity of certain regions provided an ecological opportunity for C_4 photosynthesis (Edwards et al. 2010), which allowed plants to succeed in the modern atmosphere with lower CO_2 (Sage et al. 2012). Such innovations at the base level of life's food chain provided opportunities that facilitated further expansions of life.

Regarding the source of life's food supply, we now know that it ultimately comes from fusion reactions in stars like our sun (Eddington 1920). Our sun emits 3.7×10^{26} W (Kaushika et al. 2018), less than a billionth of which (1.78×10^{17} W) strikes the earth's outer atmosphere (Wald 2009). The sun is but one of a trillion stars in the Milky Way (Odenwald 2017), which is one of two trillion galaxies in the observable universe (Conselice et al. 2016). Just on earth, a full half of the incident solar radiation (8.9×10^{16} W) is not reflected back to space nor dissipated by hydrogeological cycles, but is dissipated as heat (Davis 1990). Photosynthetic organisms today use 0.14% of this available power (1.30×10^{14} W; Steger et al. 2005), and this constitutes the primary source of power source of life (Judson 2017). Even a seven-fold increase of life's power usage would still leave 99% of that which is dissipated as heat to maintain global environmental temperatures. It seems likely, then, that life has not fully exploited the sun's power, even within the confines of maintaining the earth's life-supporting balance.

Based on these facts, I allow an alternative scheme, where there is an unlimited external energy source (Fig. 2D). The biotic "food supply" then increases by innovations in primary production. These innovations convert the abiotic free energy into biotic resources, which provide food for higher trophic levels. The consequence of an abundant abiotic resource supply is therefore a recurrent release from checks to increase, or what I call **the struggle for supremacy**.

The struggle for supremacy is a temporary phenomenon that manifests when populations escape the struggle for existence. Though infrequent, transient population increases can have major impacts on evolution. A population of bacteria that doubles once every thousand years will, in 100,000 years, either exhaust its resource supply or include more than $2^{100} \approx 10^{30}$ members, which is about equal to the number of all bacteria on earth (Wasik and Turner 2013, p. 521).

All of the advances in photosynthesis cited above involved the primary level of the food chain. Other traits may, however, increase primary production by ecological feed-

back loops. For example, in the world's oceans most of the biomass is heterotrophic (Bar-On et al. 2019), and primary-producing phytoplankton are limited by light and nutrients available in the photic zone (Sigman and Hain 2012). Heterotrophic decomposition of phytoplankton biomass drives nutrient cycling, which in turn increases primary production (Sigman and Hain 2012). Likewise, in terrestrial environments, grazers decompose dead plant material, return nutrients to base layers, return CO_2 to the atmosphere, and spread plant propagules. Evolutionary innovations that lead to additional trophic levels could thus increase primary production.

The potential for transient population increases at different trophic levels means that there is an alternative form of competition in long-term evolution. Here, the first form to exploit a resource opportunity expands in population, and diversifies into a clade of specialized species. Those who win the race to innovate gain an **incumbent** advantage (Rosenzweig and McCord 1991), which prevents others from radiating into the resource base (Simpson 1944, 1953; Benton 1987). Such an incumbent advantage could arise with the exploitation of an abiotic or biotic resource. If a strain of *Pseudomonas fluorescens* bacteria exploits the abundant nutrients provided in a laboratory environment, it will prevent the radiation of other strains (Brockhurst et al. 1997). If a plant is the first to invent an improved photosynthetic ability (Gago et al. 2020), it will win the race to innovate compared to other plants.

Factors that may trigger large-scale expansions include the novel invention of a new trait, the dispersal or movement into an unoccupied territory, or a change in climate or environment that favors an existing form that is pre-adapted to the new condition (Wright 1948; Simpson 1953; Losos 2011). The clearance of an entire zone by a natural disaster or climate change can also provide the conditions within which novel invention, preadaptation, dispersal, and further changes of environment contribute to expansion (Lidgard et al. 1993; Benton 1996; Staubwasser et al. 2018). Under the struggle for existence, in contrast, an allele that spreads may exist for thousands of generations in a single functional form before being replaced by a slightly altered allele. There is no incumbent advantage of alleles diversifying into a set of specialized alleles as there is for species.

Darwin himself tended to view the competition between higher taxa in the same way as he viewed competition within species (Simpson 1944, p. 212; Benton 1987). When we allow for resource abundance and transient population increases, however, we also allow for a prominent role of indirect competition in macroevolution that happens as a race to innovate. This does not mean that higher taxa never directly replace each other. It simply means that such replacements, where they do occur, are an incidental consequence of a competition that occurred as a race to innovate.

Natural reward

The potential for transient population increase means that those organisms that are first to win the race to innovate are **naturally rewarded** with an incumbent advantage. This suggests the possibility of natural reward as a deterministic force of evolution

separate from natural selection. How might we conceptualize this force, and what are its consequences?

To begin with, I use the term **artificial reward** to denote the supernormal profits earned by innovators in human economies (Prinsep and Biddle 1880, p. 84; Aghion and Howitt 2009, p. 7). As Aghion and Howwitt (2009), p. 7 describe it, "...the reward for innovation is monopoly profit, which comes from being able to do something that your rivals haven't yet been able to match." In this sense, the monopoly profit in human societies, which provides an artificial reward for innovation (Schumpeter 1942, p. 102), is analogous to the incumbent advantage in nature (Rosenzweig and McCord 1991), which provides a **natural** reward for innovation.

To separate the roles of natural selection and natural reward, I distinguish the roles of **invention** and **entrepreneurship**, known from studies of human innovation (Schumpeter 1942, p. 132; Schumpeter 1947, p. 152). In human technological evolution, **invention** refers to the initial origin or creation of technological novelties (Paley 2010; Grossman 2011). The process of **entrepreneurship**, in contrast, typically involves **dissemination** of inventions (Murphy 2015, pp. 70–71). For example, Steve Wozniak played the role of inventor, and Steve Jobs the role of entrepreneur in the early days of Apple Computer, because Wozniak created the first Apple computers, and Jobs spread them to markets (Wozniak 2007; Isaacson 2011). Likewise, authors often play the role of inventor and literary agents the role of entrepreneur in the origin and dissemination of literature. The entrepreneurial function is often overlooked because it does not consist of creating anything new (Schumpeter 1942, p. 132), but instead refers to the spread of inventions to new markets that demand them.

Emerging markets are often highly complex, chaotic and unpredictable based on past experiences. Therefore, the best entrepreneurial strategies are reactive rather than predictive (Christensen 1997, p. 129; Felin et al. 2014, p. 270), and many human inventions often originate through a process of conscious building combined with random error and succeed for unanticipated reasons (e.g., Wagner and Rosen 2013, p. 2). If nature operates similarly, then nature's entrepreneur may operate without foresight.

If we allow natural selection to play the role of nature's blind inventor (Jacob 1977; Dawkins 1986), and natural reward to play the role of nature's blind entrepreneur, we are led to a theory of evolution that invokes only deterministic forces (Table 1 and Fig. 3). Under this theory, the dominant situation of nature is resource abundance (Fig. 3B). Transient population increases quickly lead to resource limitation and checks to increase (Fig. 3, top). The effective resource limitation leads to a struggle for existence, natural selection, and survival of optimized alleles. There are then two consequences of natural selection (Fig. 3A). First, over intermediate time scales of a thousand to a million generations, natural selection leads to the origin of inventions. Over broader time scales, and with climate change and extinction, natural selection leads to the origin of idiosyncratic traits that appear as one arbitrary thing after another (McShea and Simpson 2011; Fig. 3A).

With natural reward, however, the recurrent potential for population increase also means that over broad time scales, populations also exist in a state of effective resource

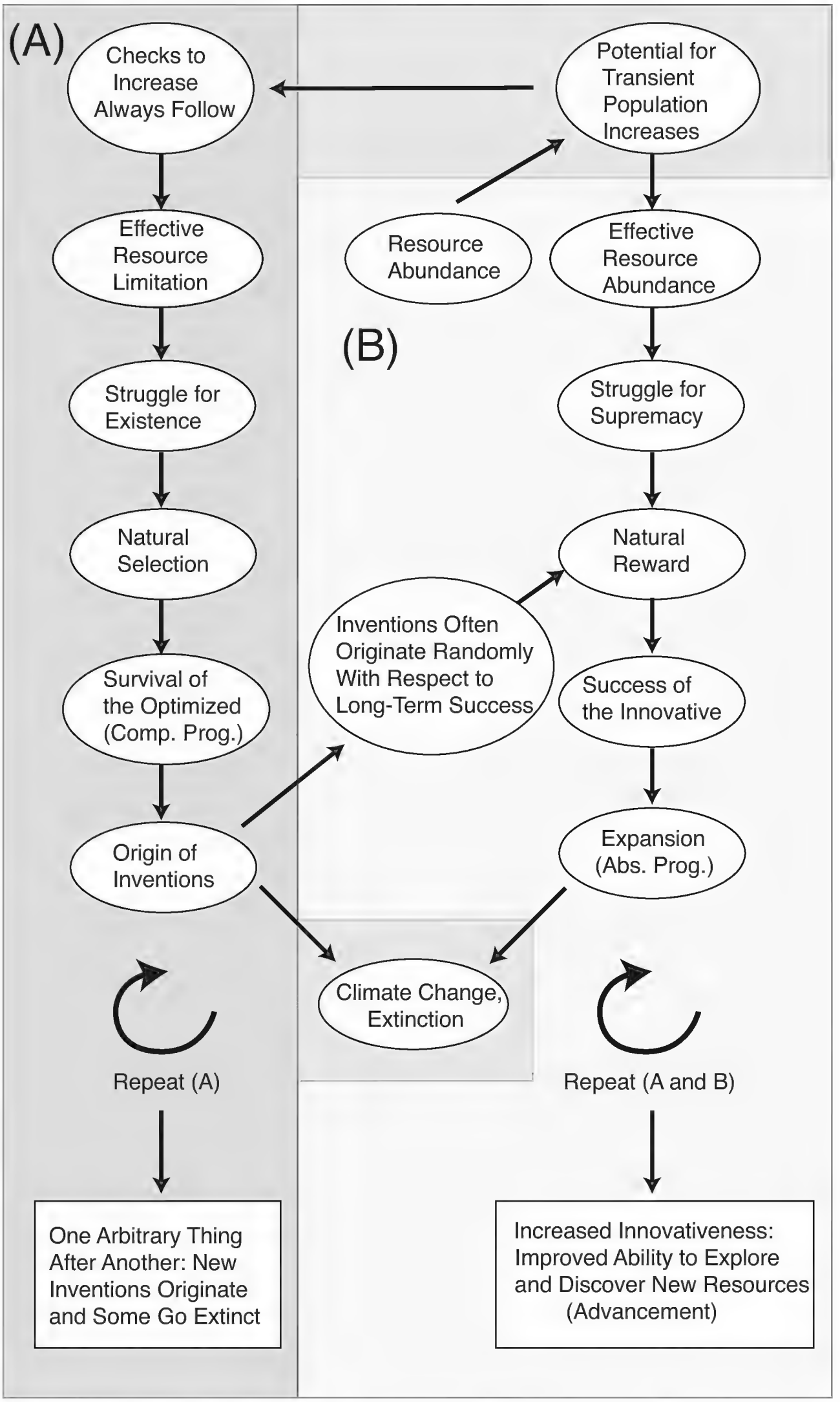
(A)
Checks to Increase Always Follow
Effective Resource Limitation
Struggle for Existence
Natural Selection
Survival of the Optimized (Comp. Prog.)
Origin of Inventions
Repeat (A)
One Arbitrary Thing After Another: New Inventions Originate and Some Go Extinct
Potential for Transient Population Increases
Resource Abundance
Effective Resource Abundance
(B)
Struggle for Supremacy
Natural Reward
Inventions Often Originate Randomly With Respect to Long-Term Success
Success of the Innovative
Expansion (Abs. Prog.)
Climate Change, Extinction
Repeat (A and B)
Increased Innovativeness: Improved Ability to Explore and Discover New Resources (Advancement)

Figure 3. Comparison of theories of natural selection and natural reward. A The theory of natural selection includes A only. **B** The theory of natural reward includes A and B, and the connection between them.

Table 1. Key concepts in relation to the deterministic forces.

	Natural selection	Natural reward
Universal energy abundance	Irrelevant	Relevant
Resource situation experienced by life	Effective resource limitation	Effective resource abundance
Resource use	Use resources already in use	Expansion to new resources
Struggle	Struggle for existence	Struggle for supremacy
Unit of competition	Alleles within species	Genetic systems shared by higher taxa (Table 2)
Typical outcome of competition	Survival of the optimized alleles ("comparative progress")	Success of the innovative genetic systems
Long-term effects (10^3–10^6 generations)	Origin of inventions through blind processes (nature's "blind inventor")	Spread of inventions that tap new markets (nature's "blind entrepreneur"), population expansion and diversification ("absolute progress")
Extremely long-term effects (cycles of 10^3–10^6 generations)	None	Buildup of traits that facilitate further exploration and discovery of resource zones ("advancement")

abundance (Fig. 3B). A state of effective resource abundance means a recurrent potential for transient population increases. These will favor those populations and genetic systems that are the first to exploit untapped resources. Here, acting as nature's blind entrepreneur, natural reward spreads inventions to those biological markets that demand them (Fig. 3B). There are then two consequences of natural reward. During transient population expansions, natural reward spreads the traits that are gradually produced by natural selection. Over vast time frames, which include multiple rounds of invention and expansion (cycles of 10^3–10^6 generations), natural reward leads to the success of innovative forms of life, which are better able to explore and discover new resources.

The success of the innovative

In contrast to the case for natural selection, the progress produced by natural reward is absolute. Under natural selection, progress occurs as a change in allele frequency that optimizes each gene to its immediate situation. The adaptive progress is comparative in the sense that it pertains only to the immediate environment (Fig. 4A). In contrast, natural reward alters the total population size of a clade of organisms sharing a particular genetic system (Fig. 4B; here I use **genetic system** to mean heritable information encoded at any level of the genetic hierarchy; Table 2). As depicted in Fig. 4C, species *A* and *B* exploit a similar resource and are thus both potentially capable of exploiting a novel resource. Only species *B* expands to exploit the resource, and its large population size, and spread over potential physical and ecological isolating barriers, causes it to produce species *C*. The taxon including species *B* and *C* (blue) is then protected by an incumbent advantage of having a set of more diversified and specialized species. Therefore, the genetic system shared by species *B* and *C* wins the race to innovate compared to that of species *A* and is naturally rewarded with an incumbent advantage.

Under this scheme, natural selection results in the survival of the optimized alleles within species, and thus the allele is the basic unit of optimization (Table 1). Natural reward, in contrast, results in the success of innovative genetic systems shared by higher

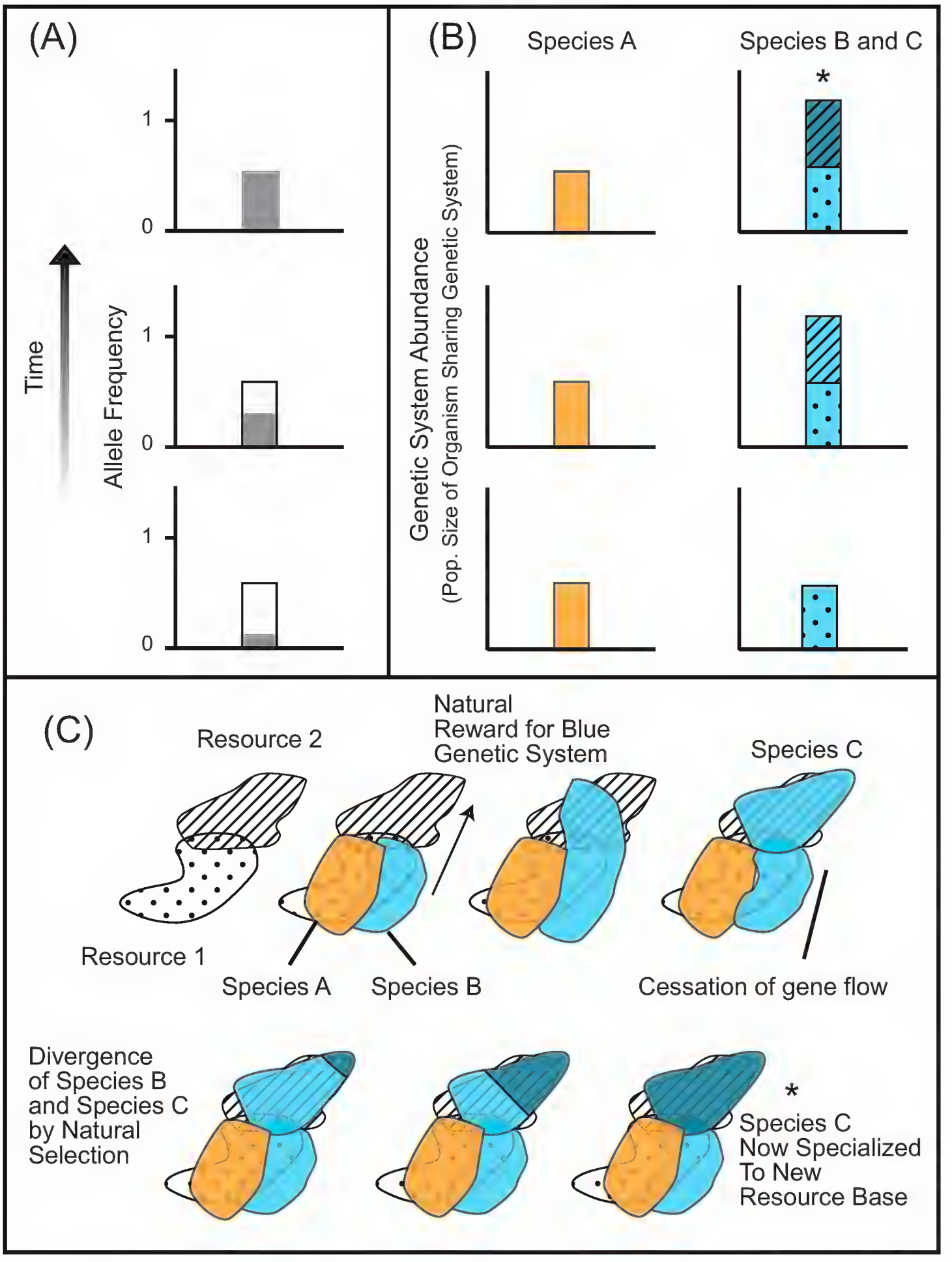

Figure 4. Consequences of natural selection and natural reward. A Natural selection causes a change in allele frequencies, and consequently optimizes each gene to its immediate environment. **B** Natural reward causes a change in the total abundance of a genetic system. Here, species A does not exploit a new resource, which species B exploits. Species B expands in population and gives rise to species C, resulting in an increase in the total abundance of the genetic system ultimately shared by species B and C (blue). **C** Diagrams showing how species depicted in (B) track to resources. Speciation between species B and C begins with a cessation of gene flow. Species C then evolves differentially by natural selection to its new resource base.

taxa. At lower levels of the genetic hierarchy, natural reward may act on gene complexes like core regulatory networks, peripheral regulatory modules, or even particular protein-coding genes shared by phyla, orders, families, genera, or species (Table 2). At broad levels, natural reward may act on more basic genetic systems, like chromosome structures or genetic codes, shared by larger groups (Table 2). Natural reward may also act on a combination of genetic systems at different levels of the genetic hierarchy, for example a regulatory network and protein-coding genes that create a novel trait or function (Benton et al. 2019). Because natural reward can operate on any level of the biological hierarchy, I use **population** in a broad sense to refer to any group of individuals, characterized by a genetic system that codes for a particular trait or function.

To be able to speak of the "success" of a population of organisms in a way that ties to the notion of absolute progress, I define **absolute progress** as **population expansion.** This is a similar definition as that used in economics, which typically equates economic **progress** with economic **expansion**, and which views increases of GDP as contributing to economic **success** (Fig. 1A; Nelson 2008; Aghion and Howitt 2009; Xong and Feng 2019). Applied to a group of living organisms, a large population size increases the chance of speciation and decreases the chance of extinction (Darwin 1859. pp. 126, 489; e.g., Hubbell 2005, p. 129), and so bears on a measure of long-term success.

As a measure of biological success, however, population size is biased toward small organisms. Thus, although we may use population size to compare the success of organisms of similar size, comparisons between organisms of different size requires a different measure. Energy flow and biomass are possible substitutes (Lotka 1922), the latter being easier to measure (Odum 1970, p. 82–83). Looking at the world today, the most successful forms of life, as judged by their biomass, are terrestrial plants, followed by bacteria, fungi, animals, archaea, protists, and viruses (Bar-On et al. 2018).

By defining absolute progress in terms of population increase, we are able to separate the measure of success from the traits that cause success. This is useful because it allows us to focus on what it means to be successful. Wasik and Turner (2013) argued that viruses are the most successful inhabitants of the planet because they are the most numerous, extremely diverse in their genetics and habits, and are extremely adaptable. In contrast, we may say that the large population size of viruses is indicative of their small size and that when we normalize for size in our measure of success by using biomass as a substitute, viruses are only about as successful as annelids or mollusks (0.2 Gt Carbon), but less successful than arthropods (1 Gt carbon; Bar-On et al. 2018). That viruses are about as successful as moderately successful animals suggests that viruses have done well despite being small, and we may hypothesize that this moderate success is caused by their adaptability, or their diversity in genetics and habits.

The advancement of life

Advancement is a sort of second-order absolute progress, conveyed by an increased ability to create or disseminate inventions. How do natural selection and natural reward, act-

Table 2. Example of hierarchical classification of genetic systems.

Level of genetic organization	Relevant population	Examples	Conservation	Effects	Refs
Standard genetic code	Most organic life on earth	Rules by which four DNA base letters with $4^3 = 64$ possible three-letter words encode 20 standard amino acids (some words are redundant)	Several deviations in natural microbes	The nature of the code affects the evolvability of all life on earth	Maynard Smith and Szathmáry (1995); Ling et al. (2015)
Basic chromosome structure	Domain	Multiple linear chromosomes in eukaryotes. One or two circular chromosomes in bacteria.	All eukaryotes have multiple linear chromosomes, deviating much in number. Most bacteria have one or two circular chromosomes. A few have linear chromosomes.	Multiple linear chromosomes allow vast expansion of regulatory ability of individual genes and modules, increased genome size, and sexual differentiation. One or a few circular chromosomes allow efficient replication.	Maynard Smith and Szathmáry (1995)
Core regulatory gene complexes ("kernels")	Kingdom and Phylum	Genetic networks controlling multicellular and multinuclear organization. Heart-field specification shared by arthropods and vertebrates.	Highly conserved and invariant. Deviation often leads to developmental catastrophe.	Determine primary kingdom and phylum-level characters that influence basic organismal structure and interaction with the environment	Davidson and Erwin (2006)
Peripheral regulatory genes that affect signal transduction systems	Class, Order, Family	*Wnt*, *Hedgehog*, *Notch* in animals	Flexible deployment, even in related species	Determine morphological pattern and size of body parts	Davidson and Erwin (2006)
Protein-coding genes under regulatory control	Genus, Species	Skeletogenic and pigment cell differentiation batteries in animals	Labile and undergo continuous renovation	Determine functional capabilities of body parts	Davidson and Erwin (2006)

ing together, yield advancement? To answer this question, I will give a possible example of advancement, which serves as the basis for hypothetico-deductive reasoning. Particularly, I discuss how mammals replaced large non-avian dinosaurs and marine reptiles.

The initial radiation of dinosaurs and marine reptiles started 240 My (Kelley and Pyenson 2015; Baron et al. 2017). By around 200 My, the mammals had appeared and were beginning to evolve the traits that would contribute to their later diversification and success (Luo 2007; Meredith et al. 2011; Wilson et al. 2012). The prior presence of the dinosaurs and marine reptiles, however, prevented mammals from radiating into terrestrial and marine environments.

The incumbent advantage of dinosaurs and marine reptiles was destroyed 66 My, when vertebrates weighing more than 50 pounds were annihilated (Archibald and Favosky 2004; Kelley and Pyenson 2015), coincident with the Chicxulub asteroid impact (Chiarenza et al. 2020). With the large dinosaurs and marine reptiles gone, terrestrial mammals, mostly placentals, rapidly gained size and radiated over the course of 10 my (Smith et al. 2010). Placental mammals then radiated into marine environments (Slater et al. 2010; Kelley and Pyenson 2015). Mammals then exploited more cold-water habitats (Bardet 1994; Slater et al. 2010), yielding a greater diversity of marine species (Kelley and Pyenson 2015), and humans exploited fossil fuels and other power sources previously not used by life (IEA 2019). Humans also now co-opt one third of terrestrial net primary production on the planet through their use of agriculture (Running 2012), and by tending crops in a way that maximizes yield, humans increase the transfer of digestible plant material to higher levels of the food chain, suggesting a large energy flow (Odum 1970, p. 48).

The replacement of dinosaurs and marine reptiles by mammals may be seen as an advancement for two reasons. First, mammals tapped into new niches and energy sources not previously used by dinosaurs and marine reptiles, suggesting a greater innovative capacity. Second, mammals have novel traits that allow the finding of new resources. At a base level, these traits include extended developmental care for young via placentae and mammae (Darwin 1872; Suzuki 2017; Wooding and Burton 2008), as well as improved intelligence, hearing, dentition, and vision (Luo 2007; Wilson et al. 2012; Archibald and Favosky 2004; Kemp 2006). In humans, these traits and others combined fortuitously, allowing tool building, vocal and written language, and cooperation at a large scale (Wallace 1871; Maynard Smith and Szathmáry 1995; Harari 2011). Most of the success of modern humans, however, paralleled the rise of world GDP during the industrial revolution (Fig. 1A). Therefore, understanding the success of humans, and in turn gaining insight on whether mammals are more advanced than dinosaurs, may depend on understanding the economic systems of humans of the past 300 y (see below).

Randomness of invention

The most important assumption of the theory of natural reward is that the complex inventions produced by natural selection are often random with respect to long-term

success. This core assumption allows natural reward to operate as a separate deterministic force. If it were true, on the other hand, that natural selection usually produces complex traits for ultimate effects, then natural reward would be largely redundant. By analogy, if allelic variants originated by mutation only in environments where those mutations were advantageous (Cairns et al. 1988), then mutation pressure would drive the spread of optimized alleles. Natural selection would be redundant in producing genetic optimization and, in seeking the simplest possible theory, natural selection could be ignored (Levit and Olsson 2006). Therefore, it is important to investigate the question of whether natural selection usually produces complex traits for ultimate effects, just as it was once important to investigate whether allelic variants originate by mutation preferentially in environments where those mutations are advantageous (Lenski and Mittler 1993).

What do we know about the origin and success of complex traits? To date, we have a detailed knowledge of the actual steps of evolution over intermediate time scales (10^3–10^6 generations) in only one famous example, that of the Lenski Long-Term Evolutionary Experiment (LTEE). A major achievement of the LTEE, coming at generation 44,000 was its detailed depiction of the origin and success of citrate metabolism (Blount et al. 2012; Quandt et al. 2014, 2015; Leon et al. 2018). All 12 replicate populations were exposed to the environmental opportunity of citrate, which was included in the nutrient broth to help the bacteria acquire iron (Blount 2017). If natural selection produces complex traits in response to environmental opportunities, then all 12 populations should have evolved citrate metabolism. However, only one population did. This suggests that natural selection has no foresight, but it could be reconciled with teleology if only a single mutation was necessary for citrate metabolism (Blount 2017, p. 161). In that case, natural selection would be responsible for optimizing to the final goal of citrate metabolism, and the difference between lineages would be explained by the random occurrence of a single rare mutation.

The LTEE showed, however, that the evolution of citrate metabolism relied on six selective steps (Fig. 5). The most important was the selection of the *gltA* mutation at step 4, which meant that the *citT* duplication was selectively advantageous during step 5, and that it persisted long enough for strong citrate metabolism to be selectively favored at step 6 (Quandt et al. 2015; Fig. 5). Therefore, it was not that natural selection optimized to a final goal of citrate metabolism, but that natural selection favored particular mutations that were advantageous in the immediate environment and stumbled upon a complex invention. The complex invention facilitated a transient population increase, which protected the population from extinction, and by generation 44,000, the citrate-metabolizing lineage was the only one left (Turner et al. 2015). As Blount (2017), p. 161 put it, "the big reward came only at the end."

A second example comes from a series of computer experiments, inspired by the "genetic art" introduced by Dawkins (1986, 1989). In a series of preliminary investigations, Secretan et al. (2008) encouraged humans to "breed" pictures on a website (www.picbreeder.com). Website visitors were given the option to hand off the fruits of their breeding programs to other website visitors, such that particular "evolutionary

	PRECONDITIONS.		***EVOLUTIONARY CONSEQUENCES. (elements afterward taken as Preconditions).***
1	GROWTH ON GLUCOSE, with acetate as a metabolic byproduct. Growth on acetate once glucose is exhausted.	}	NATURAL SELECTION FOR RAPID GLUCOSE FEEDING WITH GREATER ACETATE EXCRETION, the cost of excreting more acetate is compensated by the ability to usurp glucose more quickly.
2	MORE ACETATE IN THE ENVIRONMENT, partly because of the evolution of rapid glucose feeding before 10,000 generations.	}	NATURAL SELECTION FOR ENHANCED ACETATE METABOLISM, before 20,000 generations, a mutation in the *iclR* gene that switches to eating acetate earlier enhances acetate metabolism, and spreads.
3	ENHANCED ACETATE METABOLISM, making the lineage one mutational step away from acetate specialization.	}	NATURAL SELECTION FOR ACETATE SPECIALIZATION, around 20,000 generations, a mutation in the *acrB* gene that alters the tri-carboxylic acid (TCA) cycle improves acetate metabolism, and spreads.
4	ACETATE SPECIALIZATION, making the lineage one mutational step away from acetate super-specialization.	}	NATURAL SELECTION FOR ACETATE SUPER-SPECIALIZATION, just before 25,000 generations, a mutation in the *gltA* increases carbon flow into the TCA cycle, improving acetate metabolism, and spreads.
5	ACETATE SUPER-SPECIALIZATION, the *gltA* genetic modification improves acetate metabolism via the enzyme citrate synthase, which makes the population one selective step away from weak citrate metabolism.	}	NATURAL SELECTION FOR WEAK CITRATE METABOLISM, around 31,500 generations, a duplication of the *citT* gene activates expression of a pre-existing citrate metabolism pathway under the aerobic conditions of the experiment, and spreads.
6	WEAK CITRATE METABOLISM, not strong enough to exploit the untapped citrate resource zone, or trigger a noticeable population increase.	}	NATURAL SELECTION FOR STRONG CITRATE METABOLISM, around generation 33,000, new mutations in *gltA, dcta* and possibly other genes, enhance citrate metabolism, and spread in the population.
7	EXPLOITATION OF NOVEL RESOURCE ZONE, once hitting a key threshold, the strong citrate-metabolizing population exploits citrate in the 24-hour transfer cycle, and drastically increase in population size around generation 33, 500.	{	NATURAL REWARD FOR STRONG CITRATE METABOLISM, the massive population increase is analogous to a natural reward for innovation, here due to citrate in the medium. By generation 44,000, only the citrate metabolizers are left. One possible explanation for this is that environmental perturbations caused dwindling lineages without citrate metabolism to go extinct.

Figure 5. The sequence of steps leading to citrate metabolism in the LTEE. In the Lenski Long-Term Evolution Experiment (LTEE), the complex innovation of citrate metabolism gradually evolved by natural selection through steps 1–6, and was naturally rewarded in the 7th step for exploiting a new resource zone (see text for references).

branches" might be encouraged to diversify and branch further (Secretan et al. 2008, p. 1763). Through repeated bouts of breeding, a number of complex images appeared (Woolley and Stanley 2011; their Fig. 4; Stanley and Lehmann 2015, p. 27–28).

If it were true that complexity in nature were produced by natural selection optimizing to final goals, then it would be expected that an optimization algorithm would discover the complex images faster than the human breeders. However, an experiment employing an optimization algorithm that favored anything more closely resembling the final objective showed that after 30,000 generations of breeding, in 20 trial runs, optimization failed to breed any of the complex images. In contrast, the human breeders, with no knowledge of the final images, bred the same complex images in less than 100 generations (Woolley and Stanley 2011; their Table 1).

These results show that an optimization algorithm, artificially endowed with teleological foresight, was less likely to find its own complex design objective, than human breeders without foresight. This suggests that natural selection, acting as a blind inventor, is actually **more** likely to discover innovations than a teleological force. In support of this, Lehman and Stanley (2011) also showed that a novelty-search algorithm, which behaves more like the naïve human breeders, was more likely to "discover" complex behavioral programs that successfully navigate a maze, than an optimization algorithm.

What is the evidence from nature, however, that complex traits evolve randomly with respect to the cause for success? One example is kin recognition used for histocompatibility, which is usually cited as a prime example of kin recognition evolved to direct help to kin (Grafen 1990). However, explicit evolutionary models show that discriminatory help selects against kin recognition (Rousset and Roze 2007). Gilbert (2015) therefore proposed an alternative historical model and found that a five-step sequence of evolutionary steps would explain the evolutionary origin of a complex kin recognition system (Gilbert 2015; Fig. 6).

In his original analysis, Gilbert (2015) found detailed evidence for his predictions in stolidobranch ascidians (Fig. 7C here). Here, I present evidence that kin recognition also evolved independently in phlebobranch and aplousobranch ascidians (Fig. 7A, B). In these two other cases, there is similar evidence of transitional states predicted by Gilbert's (2015) model (Fig. 7). This suggests that kin recognition did not evolve for the ultimate apparent goal of directing help to kin, but rather through a series of selective steps that ended with discriminatory rejection being favored for avoiding the immediate expression of conflict between non-kin (Fig. 6, steps 3–5). This model suggests that kin recognition may incidentally restrict the spread of social parasites, which might contribute to the persistence and success of complex social systems (Fig. 6; Buss 1987; Metzger and Goff 2016).

Another example of a complex trait in nature is C_4 photosynthesis. Edwards (2019) argued C_4 photosynthesis evolved through four distinct steps (her Fig. 7). The first step, an increase of bundle sheath relative to mesophyll cells, must have occurred before the biochemical pathways necessary for C_4 photosynthesis. The next step, the origin of C_2 photosynthesis, involves a less-efficient $C0_2$-concentrating mechanism, the opposite of the final effect (Edwards 2019). Therefore, although C_4 photosynthesis evolved some 66 times independently in plants (Sage et al. 2011), the spread of C_4 photosynthesis is not evidence of selective pressure to survive in an atmosphere characterized by lower $C0_2$.

	PRECONDITIONS.		***EVOLUTIONARY CONSEQUENCES. (elements afterward taken as Preconditions).***
1	NET BENEFIT OF FUSION, when the **benefits of increased size, ability to** avoid overgrowth, etc., outweigh the initial costs of fusion.	}	SELECTION FOR INDISCRIMINATE FUSION, widespread fusion and, oftentimes, variability of relatedness between fusion (social) partners.
2	VARIABILITY OF RELATEDNESS BETWEEN FUSION PARTNERS AND OPPORTUNITIES FOR FAVORING KIN OR EXPLOITING NON-KIN, allowed by inhabiting the same soma **with conspecifics, and the presence of** cues indicative of relatedness.	}	SELECTION FOR DIFFERENTIAL TREATMENT BASED ON CUES CORRELATED **WITH RELATEDNESS, for the benefit of selfishly harming and cheating non-kin,** by robbing somatic resources or germline positions, and for favoring kin.
3	COSTS OF FUSION WITH THOSE DIFFERING IN CUES, resulting from the expression of harming behavior, and **net costs of within-organism conflict.**	}	SELECTION FOR MINOR HISTOCOMPATIBILITY, for avoiding fusion wither those that differ in the "treatment" cue, but only as effectively as the cue permits.
4	RESIDUAL CONFLICT WITH THOSE DIFFERING IN THE TREATEMENT CUE, because the cues may not be detectable on the outer surface of the organism; thus not useful for "social distancing" (discriminatory rejection).	}	SELECTION FOR USING A SEPARATE ("MAJOR") CUE, which is detectable at a **distance or before fusion, for the benefit of avoiding within-organisms conflict.**
5	ADVANTAGE TO RARE ALLELES OF A MAJOR HISTOCOMPATIBILITY CUE, use of a separate cue reverses the form of frequency-dependent selection acting on a cue, and rare alleles of the separate major histocompatibility cue are favored.	}	SELECTION FOR MAJOR HISTOCOMPATIBILITY CUE POLYMORPHISM (GENETIC KIN RECOGNITION), resulting in further **reduction of conflict and increase of relat**edness within the organism, yielding a precise histocompatibility system that restricts fusion to kin.
6	HYPERVARIABLE GENETIC KIN RECOGNITION SYSTEM USED FOR HISTOCOMPATIBILITY, which incidentally prevents the spread of social parasites.	{	NATURAL REWARD FOR PREVENTING THE SPREAD OF SOCIAL PARASITES. Social parasites may otherwise exploit the vast somatic resource zone of highly cooperative species.

Figure 6. The sequence of steps leading to kin recognition in Gilbert's (2015) model of histocompatibility. Histocompatibility gradually evolved by natural selection through steps 1–5, kin recognition evolving adaptively in the 5th step. Whether kin recognition used for histocompatibility is naturally rewarded in a 6th step is an open question.

These examples show that complex traits may originate randomly with respect to their causes for success. In some other cases, it would appear that the causes for origin and success are the same, and thus that nature's inventor is not really blind (e.g., examples like mimicry, camouflage, and camera-like eyes; Dawkins 1996, pp. 138–197; Bergstrom and Dugatkin pp. 89–95; Futuyma 2013, pp. 615–619; Zimmer and Emlen 2013, pp. 311–316; Suzuki 2017). However, just as it is unnecessary that mutation is **always** random with respect to selection (Dawkins 1996, p. 82), it is unnecessary that invention is **always** random with respect to reward.

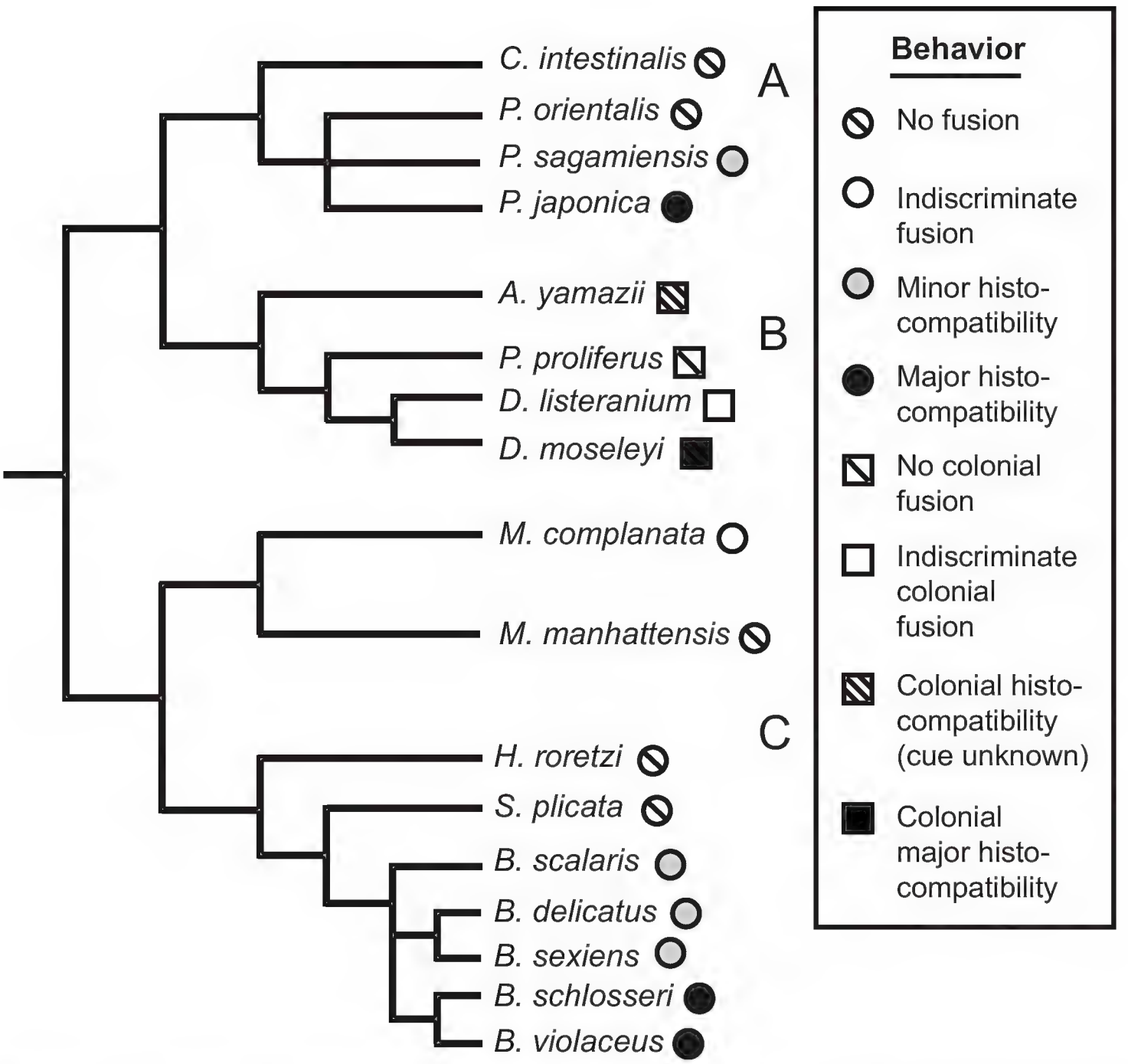

Figure 7. Cladogram of ascidians. This figure shows the transitional states predicted by Gilbert's (2015) historical model (Fig. 6). Cladogram is organized by suborders **A** Phlebobranchia, **B** Aplousobranchia, **C** Stolidobranchia, and the form of histocompatibility (fusion-rejection) behavior employed (see Appendix for methods).

Discussion

In this article, I have briefly summarized a new theory of macroevolution that invokes an alternative deterministic force, natural reward. Crucial to this theory is the assumption that the causes for origin of complex traits may be different from the causes for success, an assumption that I have discussed in the light of recent research. In this discussion, I will compare the theory of natural reward, which includes both natural selection and natural reward as deterministic forces, to a theory that includes natural selection alone as a deterministic force. I will concentrate first on the question of absolute progress, as seen from the lens of Darwin's theory, and I will then discuss the application of the theory of natural reward to the dissemination of inventions. Finally,

I will discuss the problems of the apparent sudden origins of new forms in the fossil record, and the causes for humanity's recent success.

Evolutionists going back to Darwin (1859) have derived arguments for absolute progress in terms of evolvability. The basic argument is that the long-continued action of natural selection will lead to an increase of evolvability, for example as indicated by an increase of variability or propensity to "diverge in character" (e.g., Darwin 1859, p. 118). In the only figure in "The Origin of Species", Darwin argued that there is an overall increase of variability, because the two initially variable species, A and I, give rise to 14 species after 15,000 generations (a seven-fold advantage), while the other nine non-variable species (B-H, K-L) gave rise to the same number as present at the beginning (no advantage). Darwin's "evolvability" argument explains increased ability to evolve if indeed, "the tendency to variability is in itself hereditary" (Darwin 1859, p. 118).

The basic limitation of Darwin's evolvability argument is found in most evolvability arguments since (e.g., Dawkins 1986, 1989; Lloyd and Gould 1993, etc.). The main limitation is that it assumes effective resource limitation (Fig. 2A or 2B). With effective resource limitation, an increased ability to evolve by natural selection results only in greater ability to adapt to the immediate conditions of life, but it does not lead to absolute progress (Fig. 4). The secondary limitation is that Darwin's evolvability argument focuses only on one trait, variability, which falls into a broader class of traits involved with the origin and dissemination of inventions.

The importance of resource abundance for favoring innovative traits is borne out by computer simulation. Lehman and Stanley (2013) showed that more evolvable genotypes spread in environments where population expansion was possible due to the availability of open niches. This result held even without competition within niches, suggesting a natural reward for evolvability that is separate to natural selection. Likewise, Lehman and Miikkulainen (2015) showed that the periodic opening of new niches by the sort of mass extinctions that Darwin (1859) p. 73, 489 ignored can reward traits that increase the probability of founding new niches.

Evolvability arguments similar to Darwin's also conflate the cause for origin or maintenance of a trait, with the cause for success. In addressing the problem of why sexual reproduction is widespread (Otto 2009, p. S1; Barton 2009, p. 187), for example, evolutionists typically ask why sexual reproduction originates or is maintained (*sensu* Maynard Smith 1971). Sexual reproduction may spread widely, however, for reasons that have nothing to do with origin or maintenance. For example, sexual reproduction may spread widely because it facilitates hybridization and introgression, which are a major source of genomic novelty across the domains of life (Arnold 2002; Christin et al. 2012; Soucy et al. 2015; Arnold and Kunte 2017), and contribute to adaptive radiation (Seehausen 2004; Yue et al. 2012; Wasik and Turner 2013); or because it also allows the spread of transposable elements, which are a major source of genomic novelty in eukaryotes (Feschotte 2008; Wagner and Lynch 2010; Chuong et al. 2017) and also contribute to adaptive radiation (Ricci et al. 2018). In other words, sexual reproduction may spread widely because of its transient effects on population increase, which cumulatively have vast impacts on distribution. Hybridization and

transposable elements, however, would not explain the selective origin or continual adaptive maintenance of sex, because they have detrimental effects in the short term.

The theory of natural reward also unifies traits involved with inventiveness, or the origin of complex traits, and entrepreneurship, or traits involved with their dissemination. Lehman and Stanley (2013) showed that traits that increase the probability of founding a new niche, which could include dispersal traits, increase in abundance when they contribute to population increase, but they only cause spatial sorting (*sensu* Shine et al. 2011) when they do not contribute to population increase. Familiar examples of disseminating traits are those involved with dispersal, which disseminate through space. However, traits that disseminate through time are also relevant, and these include hardy cysts, seeds, diapause stages, and stochastic phenotype switching traits (Kussell and Leibler 2005; Evans and Dennehey 2005; Shine et al. 2011). These traits can allow survival through catastrophes and can spread by exploiting novel resource zones following clearance (Harries et al. 1999). Traits involved with entrepreneurship (e.g., dispersal) are unified with traits involved with inventiveness (e.g., those affecting variability), because both are naturally rewarded by their effects on transient population increases.

Other entrepreneurial traits are hereditary systems, like the genetic code, which help disseminate inventions. The existing distribution of genetic codes suggests that all existing variants descended from a single code, which was itself fixed in the deep past (Ling et al. 2015). Usually it is assumed that natural selection optimized the genetic code, and evolutionists search for ways that the code might be optimal (Freeland and Hurst 1998). However, given that 64 three-base-pair "words" (codons) encode 20 amino acids and a punctuation mark, there are 21^{64} possible codes, meaning that arguments for optimality are almost destined to fail by many orders of magnitude (Zamudio and Jose 2017, p. 2). An alternative approach focuses on the innovative capacity of a common code. Under this perspective, early life forms that happened to specialize on the initially most abundant and useful codes gained access to the largest pools of protein innovations, leading to the fixation of a single code (Vetsigian et al. 2006). Similarly, a main explanation for the fixation of English as the worldwide scientific language is that scientific work in Britain had a major impact early during the scientific revolution of the 17th century, and English was thus an abundant scientific language. Using English then allowed scientists to gain access to the largest pools of scientific innovations (Drubin and Kellog 2012). English, however, may not be an optimal scientific language because it has a clumsy relationship between words and numbers (Dehaene 1997; Gladwell 2008).

Even without optimality, the use of a common code or language represents an advancement compared to having many codes or languages, because it enhances the capacity for further innovation sharing (e.g., as also seen in computer coding; Valverde 2016). Yet, this advancement comes at the cost of having a single language or hereditary system that may not be the best. Likewise, science often advances when new theories are useful enough for guiding new research. Yet this advancement comes at the cost of having a single framework that may not be the best of all possible frameworks in the

light of further research. This is why occasional revisions of theoretical frameworks are necessary for continued scientific progress (Kuhn 1967; Thagard 1997).

The theory of natural reward also suggests an explanation for the seeming sudden appearance of new forms in the fossil record (Darwin 1859, p. 302; Wright 1948, p. 537; Gould 2002, p. 755). Particularly, it suggests that transient population increases cause previously rare and undetectable forms to become abundant. For example, at generation 30,000 of the LTEE, the strain with the *gltA* innovation-enabling mutation was undetectable by the standard methods of detection (sensitive to 1–5% frequency; Quandt et al. 2015). The *gltA*-mutation-bearing strain then appeared suddenly in the frozen fossil record at generation 33,500, also with the *citT* and *dctA* mutations (Quandt et al. 2015; their Fig. 1). Taking the perspective of Darwin (1859), p. 279–311, the inability to find the *gltA*-bearing strain at generation 30,000 would be taken to suggest that the fossils were lost from that time period (Gould 2002, pp. 755–758). Taking the perspective of Gould (2002), p. 759–760, the apparent population stasis leading up to appearance of the *gltA*-bearing strain at generation 30,000 would be taken as evidence of stasis (Gould 2002, pp. 796–798), and by implication, saltation. In reality, however, it is not that fossils were lost, nor that saltation happened, but that the *gltA*-bearing lineage was so rare as to be undetectable, and then suddenly became abundant (Fig. 7). In support of this, the ancestor with the *gltA* mutation was detected at generation 25,000 before the *citT* and *dctA* mutations occurred. At that time, the lineage was actually quite abundant, and it then dwindled until about generation 33, 000 (Quandt et al. 2015; their figure 1).

I now revisit the question of whether there is anything about the economic systems of humans that might account for their recent success (Fig. 1A). I argue that the human invention of economic systems that create an artificial reward for innovation led to this success. The main classes of laws providing an artificial reward for innovation are patent laws, which ensure that authors and inventors are rewarded for their efforts (e.g., Queen Elizabeth I 1565; US Const. art. I, § 8, cl. 8) and contract laws, which ensure that entrepreneurs receive profits for spreading inventions to markets (Aidis et al. 2009, pp. 7, 12). Economies that lacked patent and contract laws typically either collapsed or evolved to imitate those that had them (Schlesinger 1995; Guellec and de la Potterie 2007; Park 2008). Additionally, human economic systems have also invented antitrust laws that limit the incumbent power of monopolies (Sherman Antitrust Act of 1890; Clayton Antitrust Act of 1914). Limiting the incumbent power of monopolies can promote large-scale competitions for new markets that may otherwise require economic depressions to stimulate. The use of antitrust laws therefore favors economic growth (Petersen 2013) without the economic equivalent of mass extinction.

In conclusion, Darwin's theory of evolution gave two conflicting messages, and acceptance of both messages as correct led to a schizophrenic state of modern evolutionary theory. The abnormal interpretation of reality stems from teleology, which appeals to final causes to explain design in nature and the major trends of evolution. Accepting only one of the Darwinian messages as correct allows us to resolve the Darwinian double bind. Under the extended theory of natural reward, the dual forces of natural selection and natural reward, acting as nature's blind inventor and blind entrepreneur,

led to increased innovativeness with time. Moreover, there is no longer a need to appeal to final causes to explain why life has advanced over the billions of years since its origin. Instead, advancement is explained as an expected outcome of two deterministic evolutionary forces, natural selection and natural reward, acting together without foresight for the future.

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Appendix I

The species in Fig. 7, listed from top to bottom, are *Ciona intestinalis*, *Perophora orientalis*, *Perophora sagamiensis*, *Perophora japonica*, *Aplidium yamazii*, *Polycitor proliferus*, *Diplosoma listeranium*, *Diplosoma moseleyi*, *Molgula manhattensis*, *Molgula complanata*, *Halocynthai roretzi*, *Styela plicata*, *Botryllus scalaris*, *Botryllus delicatus*, *Botryllus sexiens*, *Botryllus schlosseri*, and *Botrylloides violaceous*. I establish character states as follows. To establish whether fusion is at the multicellular or colonial level, I ask whether fusion involves blood vessel fusion or only tunic fusion, respectively (Bishop et al. 1999). Both stolidobranch and phlebobranch ascidians independently evolved coloniality, colony vascular systems, and fusion that can lead to exchange of blood cells (Bishop et al. 1999). In contrast, aplousobranch ascidians independently evolved coloniality

without colony vascular systems, where fusion may lead to use of a common tunic but not exchange of blood cells (Bishop et al. 1999). I distinguish the latter situation as **colonial** fusion, because it involves fusion of colonies but not multicellular individuals. I infer **minor histocompatibility** by the finding that rejection occurs after considerable fusion. I infer **major histocompatibility** by the finding that rejection occurs very quickly after first contact (*sensu* Gilbert 2015).

I establish phylogenetic relationships as follows. Kocot et al. (2018) found that Stolidobranchia are sister to Phlebobranchia+Aplousobranchia. For Phlebobranchia, I assume *Perophora* sp. have a more recent common ancestor than they do with *Ciona intestinalis*. For aplousobranch ascidians, I cite Yokobori et al. (2006) for the relationship between Didemnidae (including *Didemnum* sp. and *Diplosoma* sp.) and Polycitoridae (including *Polycitor proliferus*) and Polyclinidae (including *Aplidium yamazii*). For stolidobranch ascidians, Kocot et al. (2018) and Zeng et al. (2006) showed that *Styela plicata* and botryllids have a more recent common ancestor with each other than with *Halocynthai roretzi* and *Molgula* sp. They also showed that *Molgula* sp. is sister to the others. Molecular and morphological data indicate *Botryllus scalaris* is the most basal botryllid (Cohen et al. 1998; Saito et al. 2001). I follow Saito et al. (2001) in assuming *Botryllus delicatus* and *Botryllus sexiens* are sister to *B. schlosseri* and *Botrylloides violaceus*, and Cohen et al. (1998) for the other botryllid relationships.

For character states, I assume that *Ciona intestinalis* and *Perophora orientalis* do not fuse (Cohen et al. 1998), because there are no reports of fusion in *C. intestinalis* and *P. orientalis* will not fuse on growing edges (Saito et al. 1994). I also assume that *Perophora sagamiensis* has minor histocompatibility, while *Perophora japonica* has major histocompatibility, because *P. sagamiensis* most often presented delayed rejection and *P. japonica* rejects immediately (Koyama and Watanabe 1984). I classify *P. proliferus* as not fusing because, similar to *P. orientalis*, they do not fuse upon contact (Bishop et al. 1999). I classify *Diplosoma listeranium* as having indiscriminate colonial-level fusion because they always fuse tunics but not blood vessels (Bishop et al. 1999). I classify *A. yamazii* and *D. moseleyi* as having colonial histocompatibility because they fuse tunics and discriminately reject, but do not fuse blood vessels (Bishop et al. 1999). I classify *D. moseleyi* as having major histocompatibility because the colonies fuse blood vessels during fusion events, but reject immediately before or immediately after initial fusion (Mukai and Watanabe 1974).

I classify *Molgula manhattensis*, *Halocynthai roretzi*, and *Styela plicata* as not fusing because there is little evidence these species fuse in nature. *Styela plicata* fuses at a frequency of 6.4×10^{-4}, and fusion does not lead to systemic chimerism (Kingsley et al. 1989). I classify *Molgula complanata* as having "indiscriminate fusion," similar to *D. listeranium*, because *M. complanata* fuses, but does not reject (Schmidt 1982). I classify *B. scalaris* and *B. delicatus* as having minor histocompatibility because they reject only after blood vessel fusion (Saito et al. 2001; Saito and Watanabe 1982; Okuyama and Saito 2001). I classify *B. schlosseri* and *B. violaceous* as having major histocompatibility because both reject prior to blood vessel fusion (Saito et al. 1994; Cohen et al. 1998).